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# VASCULAR ANATOMY OF THE MEGASPOROPHYLLS OF CONIFERS

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(WITH 196 FIGURES)

### Introductory and historical

The megasporophyll in Coniferales has been the subject of much investigation and discussion, as on the interpretation of this structure depends to a great extent the views held in regard to the relation of living conifers to fossil forms, and the interrelation of living genera. If the scale in *Pinus*, the ligule in *Araucaria*, and the epimatium in *Podocarpus* represent a dorsal outgrowth of the bract, there is added a strong argument in support of the contention that the conifers have sprung from lycopod stock. If the megasporophyll represents a metamorphosed fertile shoot and its subtending bract, there exists a suggestive likeness to the Cordaitales, in which the presence of bracts on the shoot makes its identification as a shoot less difficult. Again, if the scale in the Abietineae represents an axillary shoot and the ligule in *Araucaria* represents a dorsal outgrowth, two other possibilities may be suggested: either the Coniferales have a double origin, or the Cordaitales included not only forms with compound strobili in which the scale is a metamorphosed structure, but also forms with simple strobili in which the scale is a ligular outgrowth of the bract. All these four views are supported by various investigators. Correlative with the views taken as to the origin of the group as a whole are the views as to the interrelation of genera; forms which may be considered as progenitors according to one theory may be the descendants according to another, or there may exist no relation.

The investigators before 1868 were concerned chiefly with gross observations of development and abnormalities. Rather

complete summaries of these investigations are given by RADAIS (2) and WORSDELL (11).

VAN TIEGHEM (9) in 1869 was the first to attack the problem from the standpoint of vascular anatomy. He studied forms from all the six large groups. He concluded that the megasporophyll in all Coniferales is a compound structure. The seminiferous scale represents the first and only leaf of an axillary shoot, as the vascular supply to the scale is arranged in an arc. The ovules are borne on the dorsal side of the leaf except in *Araucaria*, where the ovule is reflexed toward the ventral side and hence appears to be located between the bract and scale. In the Podocarpineae and Taxineae the leaf is reduced to such an extent that it is represented practically only by the ovule. In *Podocarpus* the leaf is folded on its dorsal surface to form an anatropous ovule, while in *Pherosphaera*, species of *Dacrydium*, *Phyllocladus*, and the Taxineae, the leaf remains erect and the ovule is orthotropous. The inversion of the ovule in certain forms is probably related to the greater elongation of the sporophyll beneath the ovular insertion in those forms.

STRASBURGER (6, 7) in 1872 and 1879 gave comprehensive descriptions of forms from all the groups. He held that in all cases the ovule-bearing organ is an axillary structure. In *Taxus* and *Torreya* the ovule is borne at the end of a secondary leafy shoot; in *Cephalotaxus* the secondary shoots are reduced to ovules. In the podocarps the secondary shoot is leafless and often reduced to an ovule as in *Phyllocladus*, or provided with a stalk as in *Dacrydium* and *Podocarpus*. In the Araucarineae it appears as if a stalk bearing an inverted ovule were fused to the dorsal side of the bract. In *Cunninghamia*, which he classified with the Araucarineae, there is a fusion of an inflorescence to the bract. In the Abietineae the scale is a flattened axillary structure which is folded inward and hence bears the ovules inverted. The two ovules suggest that the axillary shoot is an inflorescence, a primary and two secondary shoots similar to the two-flowered inflorescence in *Cephalotaxus*. In the Cupressineae and Taxodineae the scale and bract are fully welded together. Where many ovules occur, as in *Cupressus*, he left it undecided whether the ovules represent

a reduced branch system, or the large number of ovules is a new feature.

RADAIS (2) in 1894 made a rather intensive study of a number of cones of the Abietineae and Taxodineae. He notes that the bundles to bract and scale are distinct in origin in the Abietineae, *Sciadopitys*, and some of the Taxodineae, as *Cryptomeria*, *Taxodium*, and *Sequoia*, and how this distinctness is on its way to obliteration in species of *Arthrotaxis* and more so in *Cunninghamia*, and is lost in *Araucaria Rulei*.

WORSDELL (10, 11) in 1899 made a comparative study of types from the different tribes. He believes that in the megasporophyll in all conifers there is an axillary structure concerned. Speaking of *Araucaria* he says:

> Holding to the theory of the axillary bud as the explanation of the structure of the appendage of the cone in *Araucaria*, I believe, with CELAKOVSKY, that the ligule represents the seminiferous scale which is itself the vegetatively developed outer integument of a sporangium situated in the anterior position on an axillary bud. This outer integument has become almost completely fused with the subtending bract in *Araucaria*, completely so in *Agathis*.

Concerning the Taxeae and Podocarpeae he says:

> The Taxeae differ from the other groups in the fact that the sporangia occur in a position terminal instead of lateral to the axis on which they are borne. The anatomy points clearly to the fact that no axial foliar appendage of any kind exists upon which the sporangia are inserted, the cylinder of the axis being directly continuous into the base of the sporangium. This latter difference, however, amounts to very little if we regard, with CELAKOVSKY, the seminiferous scale of the other groups as being the morphological equivalent of the outer integument of the Taxeae, which has become, with the exception of Podocarpeae, vegetatively developed. In the Podocarpeae the relationship is precisely the same as in the Taxeae, with the exception of the axillary instead of terminal position of the sporangium. In this order the bundle system belonging to the sporangium (which is in all the other groups the sole representative of the sporophyll according to the view I here adopt) becomes obvious, owing to the fact that the latter gets by the basal intercalary growth on to the upper part of the bract. In the four other groups the bundle system pertaining to the vegetative development of their outer integuments, which, in the form of the widely expanded seminiferous scale, possesses a pronounced vascular tissue.

SEWARD and FORD (3) in 1906, in a somewhat extensive article on living and fossil Araucarineae, offer no interpretation of the

megasporophyll in the Abietineae, but in the Araucarineae they consider it as a simple structure which may or may not be homologous with the double structure in other conifers. They regard the Araucarineae as one of the oldest if not the oldest of the conifers. They favor the lycopod origin of the Araucarineae and set them apart under the name of Araucariales.

THOMSON (8) in 1909, in a paper on *Saxegothaea* and *Microcachrys*, admits that the brachyblast theory is inevitable in the Abietineae, Taxodineae, and Cupressineae. Accepting BRAUN'S conception that the scale in the Abietineae represents the first and only two leaves of an abortive shoot, which have fused by their adaxial margins, he says:

> The first inversion is explained and the ovules in the group are borne on the morphological under side. The second inversion is analogous to the single one in *Saxegothaea* and of the nature of a sporangial supply. There are then two great groups of conifers from the standpoint of this study, the simple and the complex scaled series. Both forms have the ovules on the physiologically upper surface, a position rendered almost imperative by the necessities of the seed habit. This position however has been attained in two very different ways.

STILES (5) in 1912 investigated several species of *Podocarpus*. He concludes that the original position of the ovule was erect and axillary as in *Pherosphaera*, but that owing to growth of the scale at the base of the sporophyll it has been carried away from the axis. As a result it has become inverted, and correlated with the inversion is probably the development of an incomplete epimatium.

> Whether this epimatium is an outgrowth of ovular or sporophyll tissue it is at present impossible to say. The evidence of development in *Saxegothaea* and *Microcachrys* suggests the former, while a somewhat older state in *Dacrydium cupressinum* suggests the latter.

In the latter form the ovule is borne on the epimatium, while in *Podocarpus* the epimatium has elongated into a stalk. The development of a strong and independent vascular supply in the epimatium he thinks is the result of a required need of a larger ovule. The epimatium in the podocarps and the scale in the Abietineae are homologous, but both are new structures. Both these complicated structures have been derived from a simple sporophyll.

The Abietineae and Podocarpineae have come from a common primitive stock. The Abietineae are more advanced in the development of the scale, but more primitive in holding on to a perfect cone. "The evidence at present is much in favor of the lycopodean ancestry of the conifers." He has little faith in the brachyblast theory, as it depends for its support mostly on abnormalities and the vascular anatomy of the cone scales. "But abnormalities, especially when they are supposed to be more or less of the nature of reversions, afford by themselves unsatisfactory evidence of phylogeny." Vascular anatomy disproves the double nature of the megasporophyll of the araucarians and podocarps, except in some species in the latter, and there the compound structure is of recent origin.

SINNOTT (4) in 1913 gave a very clear account of the strobilar anatomy in a number of podocarps. He is of the opinion that the podocarps and araucarians, along somewhat parallel lines of development, have been evolved from ancient abietinean stock. The scale in the Abietineae, the ligule in the araucarians, and the epimatium in the podocarps are all homologous and vestiges of an axillary shoot, and a simple sporophyll has arisen either by the fusion of both of its parts or by the abortion of one. Of the podocarps he considers those most primitive in which the epimatium is well developed and has a strong vascular supply, as *Podocarpus;* and those most advanced in which there is a reduced epimatium, as *Dacrydium.* In *Podocarpus dacrydiodes* there is a definite step in the direction of *Saxegothaea, Microcachrys,* and *Pherosphaera.* The resemblance in reproductive structures between certain members of the Podocarpineae and *Cephalotaxus,* the most primitive genus of the Taxineae, suggests that the latter family has arisen from some ancient member of the Podocarpineae.

EAMES (1) in 1913, in a paper on *Agathis,* considered also the megasporophyll situation in other conifer groups and concludes that the megasporophyll is compound in origin in all Coniferales. "Even within themselves the Araucarineae show a complete series from a form with strobilar units of a distinctly double nature to one most simple through reduction." EAMES has traced a similar reduction in the Taxodineae.

## Investigation

### ABIETINEAE

The ovulate strobilus in all the Abietineae is composed of a comparatively large number of sporophylls. The sporophyll here is obviously composed of two organs. In some forms, as *Keteleeria* and *Pseudotsuga*, each of the three-pronged bracts is reflexed over the scales below, giving the strobilus a bristly appearance; while in others, as *Cedrus Libani*, the bract is a minute flap, and its bundle dies before it reaches the free portion. Between these two extremes are many intermediate forms. That the bract is a modified leaf seems evident at least in some genera. In *Pseudotsuga* and *Larix* there is a gradual transition from ordinary foliage leaves to bracts of a well developed sporophyll; and in abnormal cones of *Picea*, *Larix*, etc., the bracts are like the vegetative leaves. The scale is well developed in all the Abietineae.

The vascular anatomy of the megasporophyll is less variable in the different genera of the Abietineae than is the case in any of the other five groups.

In the lower one-third or more of the strobilus of *Pinus maritima* and *P. Banksiana* there is a general sterilization, beginning with failure of the ovules to produce seed, followed lower down by the abortion of the ovules, and finally at the base of the strobilus the reduction in size and final disappearance of bract or scale or both. In *P. Banksiana* the bract disappears before the scale, but both are finally lost, and between the lowest ovuliferous scales and the bud scales is a region where the strobilus stalk is smooth except for slight elevations (fig. 2). Each of these elevations is supplied with a small vascular strand and suggests a vestige of a megasporophyll. In *P. maritima* only the scale suffers reduction and loss, and the bract, reduced throughout the strobilus, increases in size toward the base (fig. 1).

Correlative with the sterilization and reduction of the appendages in the lower portion of the strobilus are variations in mode of origin of their vascular supplies (figs. 3–29). In the upper half of the strobilus the bract supply originates as a single bundle at the base of the cylinder gap. The scale originates as three or four bundles instead of two as in other Abietineae, one at each side of the
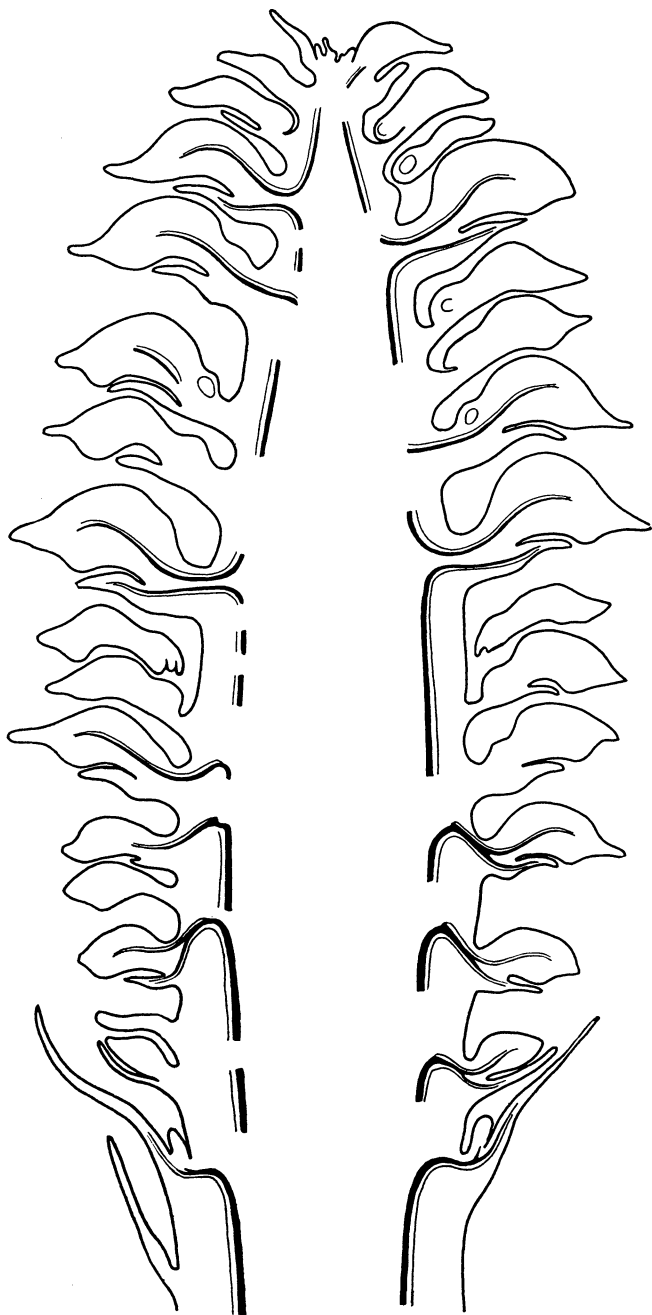
Fig. 1.—*Pinus maritima:* longitudinal section of ovulate strobilus; vascular supplies to bract and scale of each sporophyll, separated in cortex of strobilus by mass of parenchyma in upper portion, approach one another near middle and merge in lower portion of strobilus; in lower portion of strobilus scale decreases in size, while bract becomes comparatively larger.

gap some distance above the bract bundle, and above these again one at each side of gap, or one at one side only.   The two uppermost
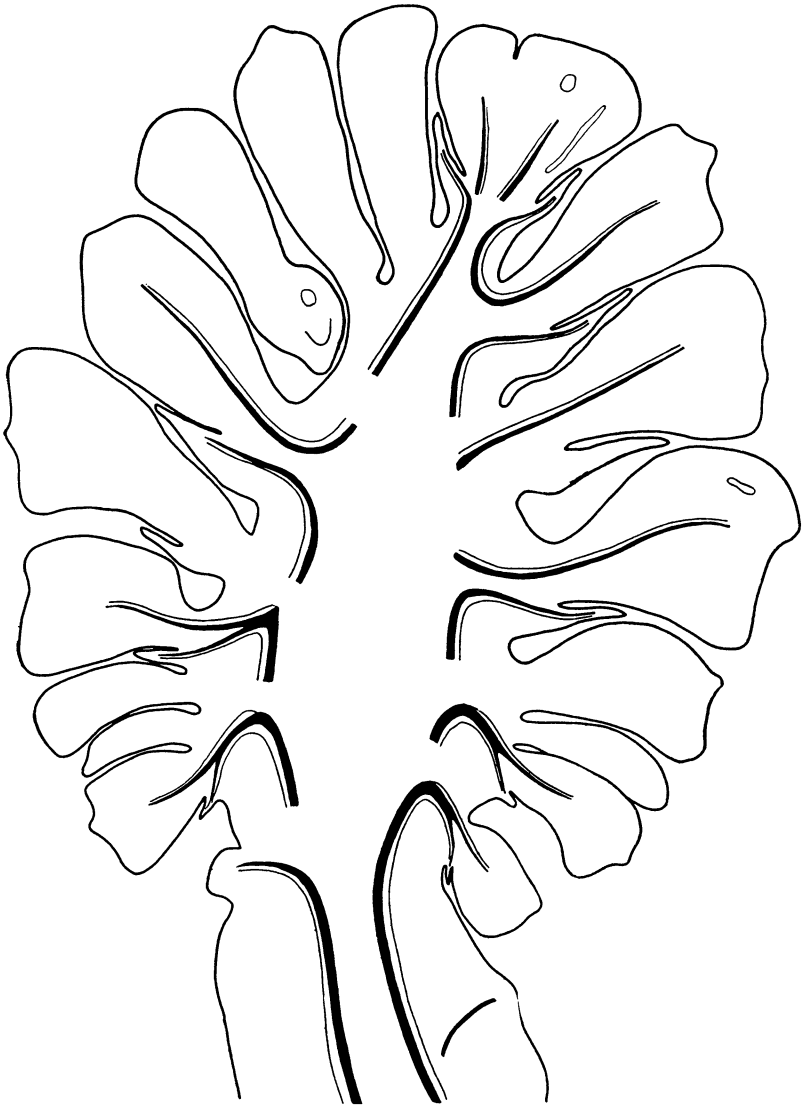


FIG. 2.—*Pinus Banksiana:* longitudinal section of ovulate strobilus; bract and scale supplies, as in *P. maritima*, separated in upper region of strobilus but become merged in lower; unlike *P. maritima*, bract becomes very small in lowest sporophylls; beneath lowest sporophylls are humps, each supplied with a bundle.

bundles soon unite into one, so that four bundles in all with xylem facing result; the lower passes undivided to the end of the bract, the three remaining spread out and give rise in the scale to a row of inverted bundles, seven or more in *P. maritima*, twelve or more in *P. Banksiana*. No branches are seen to bend toward either of the two inverted ovules. Below the middle of the strobilus the uppermost one or two bundles, as the case may be, originate near the lower scale bundles or become united with the latter so that the scale supply starts as two bundles. One of the two bundles soon divides, so that four bundles including that of the bract result; the subsequent course in the appendages is as described before. In the lower sporophyll, the scale supply originates as one or two bundles very near the bract bundle. In the lowest sporophylls the bract and scale supply originates as a single bundle at the base of the gap. In either case there is a subsequent separation into four bundles which supply their respective appendages as before described. In this region of the strobilus the four bundles remain closer together in their course through the cortex than is the case in the upper. In *P. Banksiana* the phloem is continuous around the four xylem strands, which except for a few parenchyma cells would form a solid xylem strand. Near the base of the strobilus, in this species, where the sporophyll supply begins as a single bundle, the xylem creeps around its protoxylem as a pivot and the phloem about the xylem, so that a concentric bundle results. On nearing the appendage the bundle drops into four. In this species the gaps are small, owing to a shortening of the strobilus axis. In both species the sporophyll supply takes a diagonal downward course through the cortex in the lower part of the strobilus, in contrast to the diagonal upward course taken near the tip. This is also likely due to a shortening of the strobilus axis and a consequent crowding of the appendages.

For the sake of comparison, the anatomy of a young vegetative shoot was investigated. In *P. maritima* and *P. Banksiana* (figs. 30–35), whether the bud is to give rise to a spur shoot or a long branch, a single bundle springs from the base of the cylinder gap and supplies the bract, while two other bundles, one at each side of the gap, supply the bud. The bud bundles increase in size and

divide, giving rise to a semicircle of bundles with xylem on the
concave side, facing the xylem of the bract bundle.   The semicircle
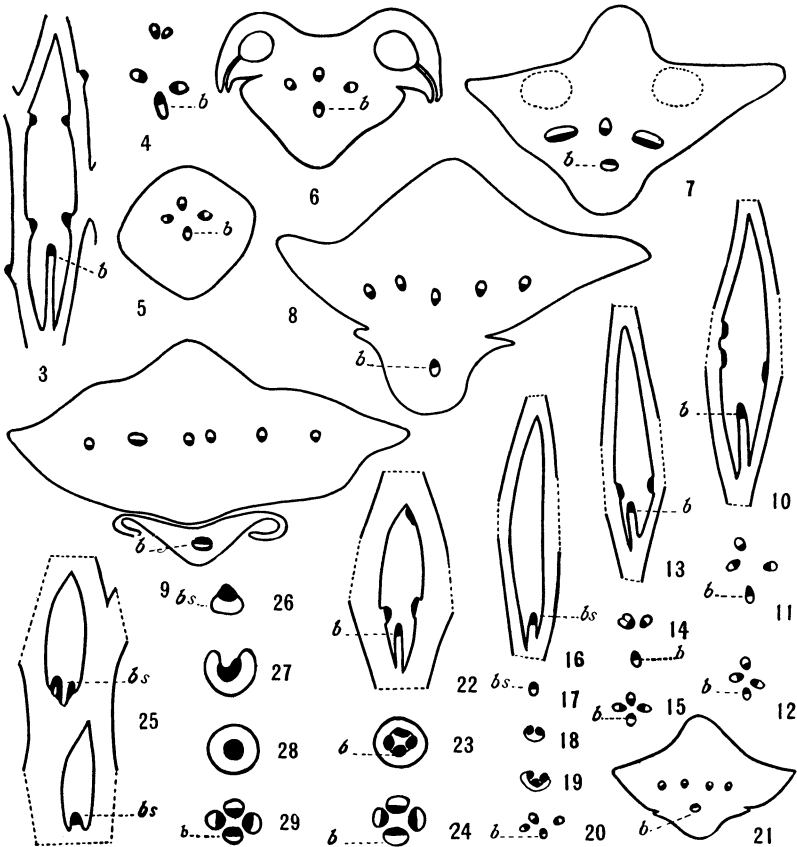


FIGS. 3–21.—*Pinus maritima:* figs. 3–9, course of bundles to bract and scale in
upper half of strobilus; fig. 3, origin of bract bundle (*b*) and scale bundles (4 remaining)
in strobilus cylinder; fig. 4, two upper bundles uniting; figs. 5–9, transverse sections
of sporophyll, bract bundle remaining undivided, scale bundles giving rise to several
bundles; figs. 10–12 and figs. 13–15, from lower half of strobilus, scale bundles decreas-
ing in number and originating nearer to bract bundle as base of cone is approached:
figs. 16–20, from lowest sporophylls, bract and scale bundles (*bs*) one in origin; fig.
21, transverse section of one of lowest sporophylls;  ×16.

FIGS. 22–29.—*Pinus Banksiana:* figs. 22–24, from middle of cone, bundles closing
up to form concentric cylinder; figs. 25–29, from lower portion of cone, phloem creeps
about xylem so that concentric bundle is formed;  ×34.

In all cases four bundles result (figs. 5, 12, 15, 20, 24, 29), the lower supplying
the bract, the remaining three the scale.

gradually approaches a circle, and in a slightly older bud closes to form the cylinder of the shoot. The bud is united with the bract at its base, and the general appearance of a young bud and its subtending bract is suggestive of a young abietinean sporophyll.
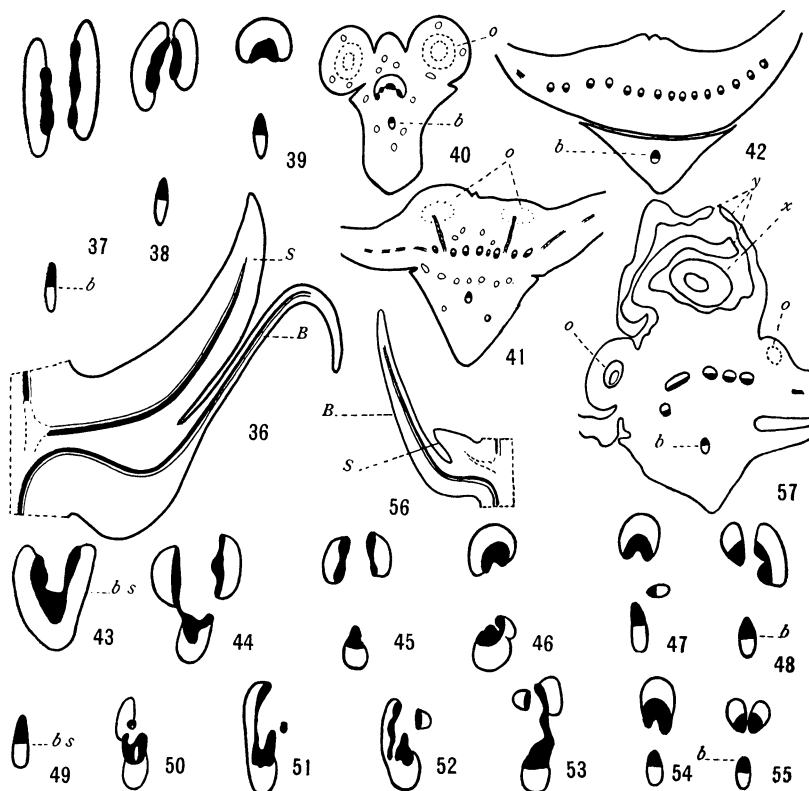
In *Keteleeria Fortunei* (figs. 36–57), one bundle originates near the base of the gap in the strobilus cylinder and supplies the bract. It remains undivided throughout its course. Two bundles, one
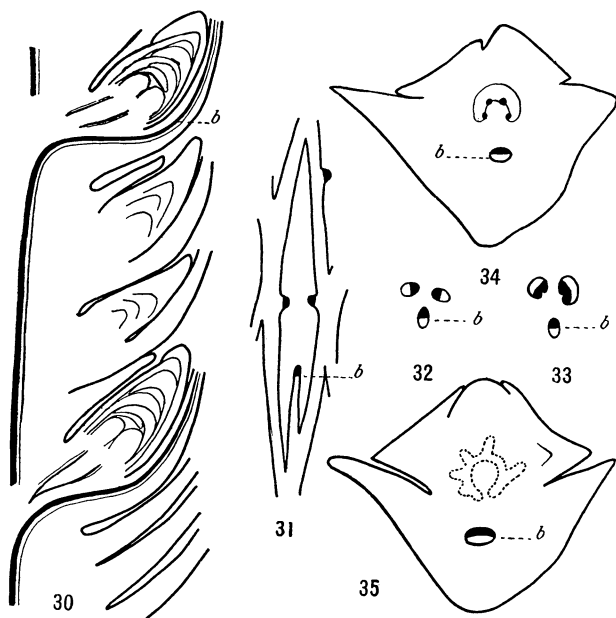


FIGS. 30–35.—*Pinus Banksiana*, vegetative bud: fig. 30, radial longitudinal section of lower portion of young vegetative branch; a vegetative bud in axil of each bract except at base of branch; fig. 31, origin of bract (*b*) and bud bundles; figs. 32–35, transverse sections, young bundles of bud beginning to form cylinder of branch; ×16.

from each side of the gap, supply the scale. The two bundles soon unite, forming one inverted bundle, that is, its xylem faces the xylem of the bract. The inverted bundle then breaks, forming a semicircle of bundles which spread and divide, forming in the scale a row of sixteen or more bundles. Near the ovular insertion a small concentric branch is given off to each of the two inverted ovules.

In the lower sporophylls the bract and scale bundles originate
in close proximity at the base of the gap.    In the lowest sporophylls
the vascular supplies to both organs originate as one bundle, and



FIGS. 36–57.—*Keteleeria Fortunei:* fig. 36, longitudinal section of sporophyll,
×16; figs. 37–42, transverse sections of sporophyll from upper half of strobilus;
figs. 36–39, two scale bundles divide actively, a single strand is given off to each ovule
(fig. 41, *o*), ×7; figs. 43–48, from one of lower sporophylls, bract and scale bundles,
close together in origin (fig. 47), gradually separate, ×34; figs. 49–55, from one of
lowest sporophylls, bract and scale bundles united in origin gradually become distinct,
×34; fig. 56, longitudinal section of young sporophyll, scale (*S*) still comparatively
small, ×7; fig. 57, transverse section of one of lowest sporophylls showing outgrowths
(*x, y*) between ovules (*o*), ×16.

the two systems separate later for their respective organs.    In
some of the lowest sporophylls the scale supply begins blindly in
the scale.

Between the ovules of the lower sporophylls is found an out-growth which suggests an ovule with a poorly developed nucellus. At each side of and behind this median outgrowth are others which are more bractlike. In some of these xylem cells are present. Whether these abnormal excrescences mean reversions to ancestral features may be difficult to determine. The young strobilus shows no such outgrowths.

<div style="text-align:center">CUPRESSINEAE</div>

The general features of the ovulate strobilus in the Cupressineae are the great reduction in the number of the sporophylls, the cyclic arrangement of the sporophylls, complete coalescence of bract and scale, and erect ovules variable in number.

The strobilus of *Cupressus Benthamii* (figs. 58–70) is composed of four decussate pairs of sporophylls. Many erect ovules are packed at the base of each sporophyll. At the megaspore mother cell stage the only evidence of the scale is a slight elevation back of the ovules and the differentiation of the scale supply near the strobilus cylinder. In somewhat later stages the free part of the scale projects outward almost as prominently as that of the bract. Contact and interlocking of epidermal cells takes place between neighboring sporophylls in such a way that the ovules become entirely inclosed.

The vascular anatomy is slightly variable in the individual sporophylls of a strobilus. As in other cyclic forms, the cylinder gap fails to close after the departure of the appendage vascular supply, and hence is continuous with the one above and below. The bract supply may arise as a single strand at one side of the continuous gap, or as two, one from each side of the gap, in which latter case the two unite into one. The scale supply originates as two bundles, one from each side some distance above the bract supply. In other cases two bundles, one from each side of the gap, compose both bract and scale supply. A strand may be given off from one of the bundles to form the bract bundle, or a strand may be given off from each bundle and the two strands unite to form the bract bundle. Whatever may be the origin, the bract bundle remains undivided to the tip of the bract. The scale bundles divide

actively; the majority come to lie near the dorsal side of the
sporophyll and have inverted orientation of xylem and phloem,
but several twist around to each side of the bract bundle and have
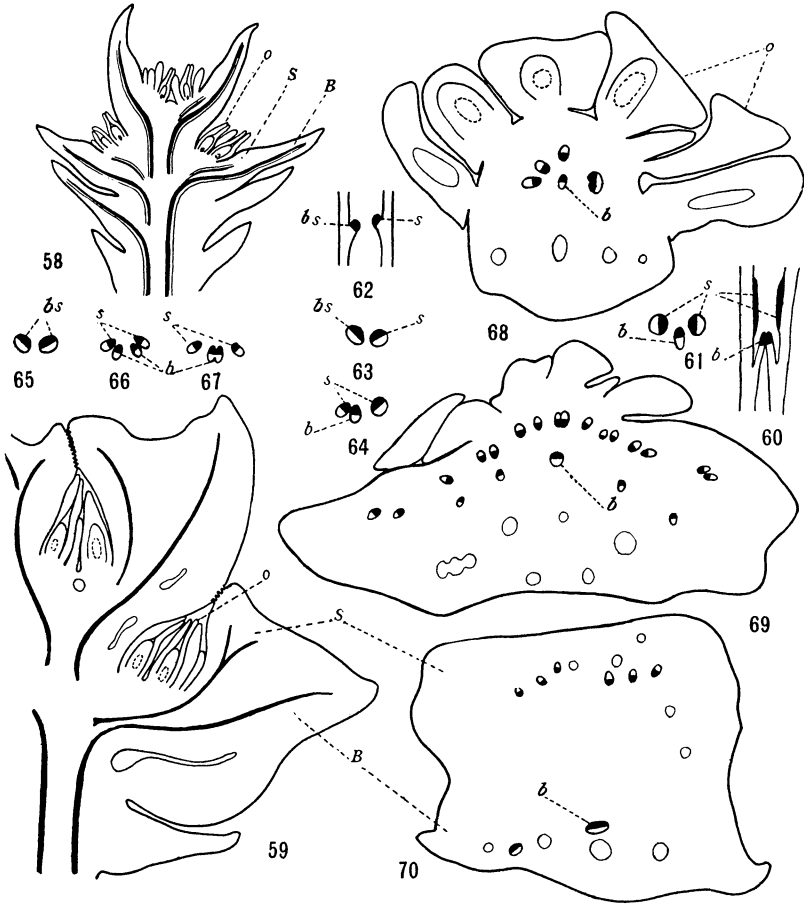


FIGS. 58–70.—*Cupressus Benthamii:* fig. 58, longitudinal section of young stro-
bilus, scale (*S*) evident only by slight elevations on upper side of sporophyll, and begin-
ning of scale bundles; fig. 59, longitudinal section of older strobilus, scale (*S*) evident
but incorporated with tissues of bract (*B*), ×7; figs. 60–67, three methods of origin of
sporophyll bundles; figs. 60, 61, bract (*b*) and scale bundles (*s*) distinct in cylinder
gap; figs. 62–64, bract bundle derived from one of scale bundles (*bs*); figs. 65–67,
bract bundle derived from both scale bundles (*bs*); figs. 68–70, transverse sections of
sporophyll, scale bundles divide vigorously, some scale bundles persist in bract portion
(fig. 70, *B*), ×16; *o*, ovule.

the same orientation of parts as the latter bundle. A fact to be noted in the further course of the bundles is that some of the lower scale bundles extend into the bract, though not as far as the bract bundle.

The ovulate strobilus of *Thuja occidentalis* (figs. 71–89) consists of about five decussate pairs of sporophylls. The two lower pairs are sterile, the third may have only one ovule to each sporophyll, the fourth two ovules to the sporophyll, and the fifth is sterile. The tissues of the bract and scale are so closely welded that it is impossible to distinguish one from the other except at the very tip. In the upper fertile pair of sporophylls the vascular supplies to bract and scale are distinct in origin. The supply of the first arises as one bundle at one side of the continuous gap; that of the latter as two bundles, one at each side and at a higher level. The bract bundle does not divide; the scale bundles give rise to numerous bundles, a few of which become inverted and lie near the dorsal side of the sporophyll; the majority, together with the bract bundle, form an irregular lower row of inverted bundles. In the two sterile pairs at the base, the bract and scale supply have their beginning as one bundle at one side of the long gap. This bundle soon drops into three, the median one supplying the bract, the two lateral the scale. The further course is as described before for the upper fertile sporophyll. In the lower fertile sporophyll is found a combination of the two methods of bundle origin mentioned. One of the scale bundles rises separately, but the other is combined with the bract bundle and rises at a lower level; it later separates from the bract bundle. The sterile tip pair of sporophylls receives the last two bundles of the strobilus axis. One bundle goes to each sporophyll, and drops into three bundles which divide further.

The strobilus of *Chamaecyparis Lawsoniana* (figs. 90–104) consists of about four pairs of sporophylls. In the cone represented in cross-section (figs. 100, 101), one of the lowest sporophylls has one lateral ovule, each of the sporophylls of the second pair two lateral ovules, and each of the third pair one median ovule; the fourth pair is sterile. In the early free-nuclear stage the scale is apparent only as a slight elevation on the dorsal side of the bract, which at this stage is almost straight. At a little later stage
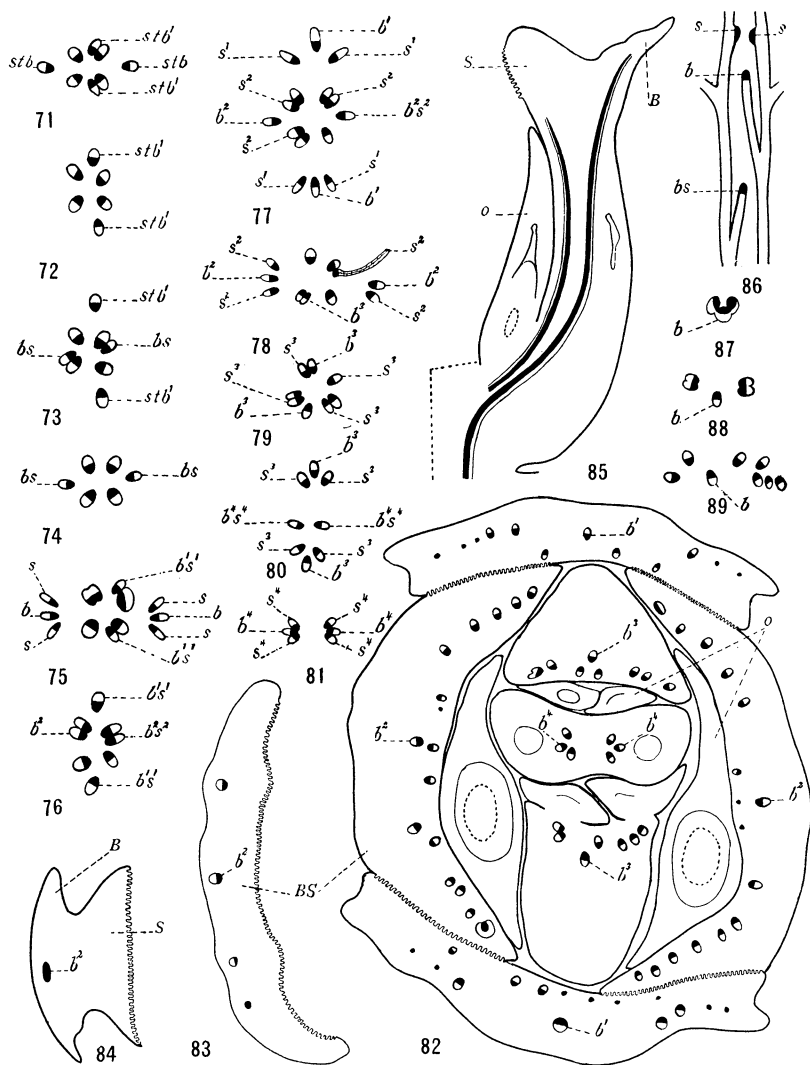
FIGS. 71–89.—*Thuja occidentalis:* figs. 71–81, transverse section of strobilus axis, showing origin of sterile bract bundles (*stb*, *stb$^1$*) below cone, bract bundles (*b-b$^4$*) of sporophylls, and scale bundles (*s-s$^4$*); fig. 82, transverse section of same strobilus, many of scale bundles become oriented like bract bundle, two pairs of sporophylls fertile, one pair bearing one ovule per sporophyll, the other two ovules; figs. 83, 84, transverse sections near tip of sporophyll, bract (*B*) and scale (*S*) beginning to separate; fig. 85, longitudinal section of sporophyll, bract (*B*) and scale (*S*) closely united; figs. 86–89, sections parallel to cone axis; fig. 86, bract (*b*) and scale (*s*) bundles distinct in origin in upper part of strobilus, united in lower (*bs*); figs. 87–89, bract bundle separating from scale bundles; ×16.
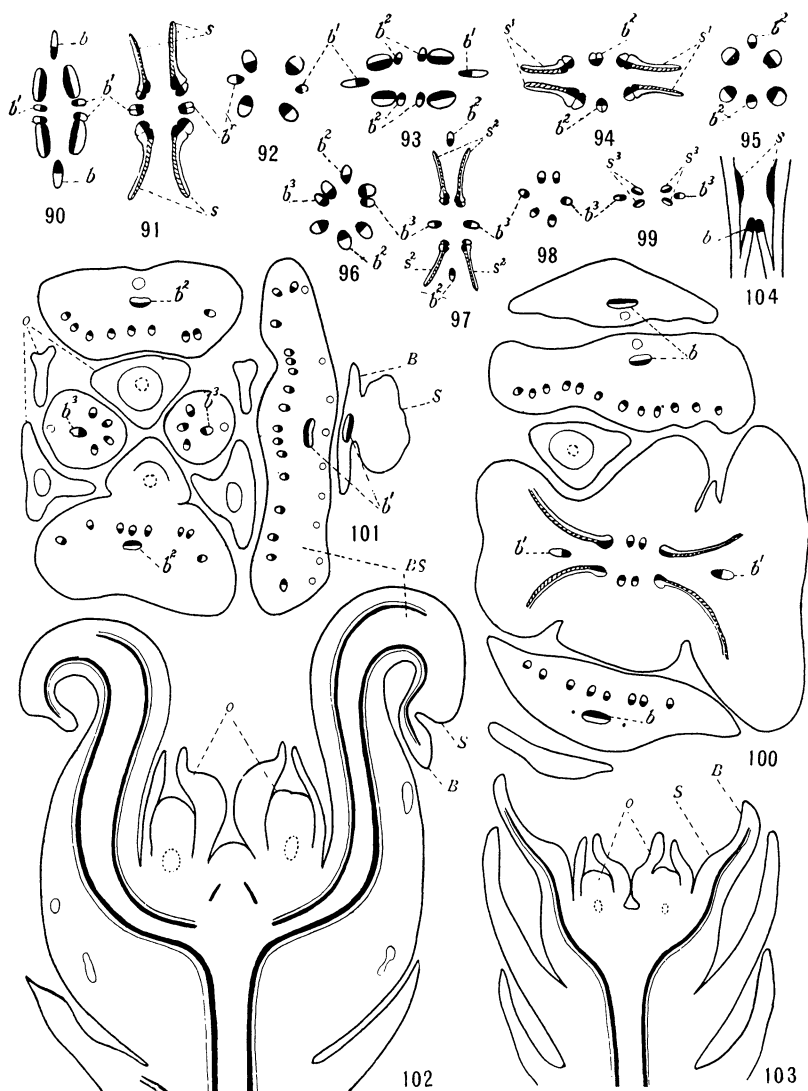
Figs. 90–104.—*Chamaecyparis Lawsoniana:* figs. 90–99, transverse sections of strobilus axis, showing origin of bract ($b$–$b^3$) and scale ($s$–$s^3$) bundles; figs. 100, 101, transverse sections of same strobilus, scale bundles remain close to dorsal side; one of sporophylls of lowest pair bears one lateral ovule, each of second pair two lateral ovules, each of third one median ovule, fourth pair sterile; fig. 102, longitudinal section of strobilus, bract (*B*) and scale (*S*) separate only at recurved tip of sporophyll; fig. 103, longitudinal section of younger strobilus, scale (*S*) evident as slight elevation on dorsal side; fig. 104, origin of bract (*b*) and scale bundles (*s*) in cylinder gap; ×16.

the growth on the dorsal side of the sporophyll is very marked, resulting in the deflexing of the coalesced bract and scale. The bract is free only at the tip of the deflexed portion. The vascular systems to the bract and scale are distinct from the strobilus cylinder. The bract bundle remains single to the tip of the bract. The two scale bundles end in a dorsal row of numerous inverted bundles. The flank bundle may turn partly and lie nearer the ventral side of the appendage.

The strobilus of *Juniperus communis* (figs. 105–113) consists of a whorl of three sporophylls united at the base and surrounding three ovules. In the older stage the sporophylls coalesce also at the tip, forming a fleshy berry-like body. The coalescence of bract and scale is complete.

After the traces to the three bracts beneath the sporophylls have left the cylinder, each of the three remaining bundles divides into three; the median or bract bundle proceeds undivided into the bract; the two lateral or scale bundles divide, giving off some bundles to the dorsal side of sporophyll and some to ventral in such way that, including bract bundle, an oval ring of bundles with xylem facing is formed.

## TAXODINEAE

The general features of the ovulate strobilus in the Taxodineae are spiral arrangement of sporophylls, reduction in number of sporophylls in some forms, considerable coalescence of bract and scale, and varying number and orientation of ovules.

In *Cryptomeria japonica* (figs. 114–128) the axis of the young strobilus is very short and the sporophylls are crowded at the broadened summit. The ovules at this stage appear to be inserted on the strobilus axis. The scale begins its development as four to six lobes between the ovules and the dorsal side of the bract. In an older stage the axis has elongated, forming a globose cone. The erect ovules, usually three in number, are definitely inserted on the sporophyll. The lobed scale is united for two-thirds of its length to the bract. In the upper portion of the cone three bundles leave the axis for the sporophyll; one at the base of the gap to supply the bract, and one from each side of gap to supply the scale.

The two scale bundles divide, resulting in the sporophyll in a ring of bundles with xylem facing inward. Included in the lower portion of the ring is the bract bundle. One and sometimes two bundles enter each lobe of the scale. A number of the scale bundles
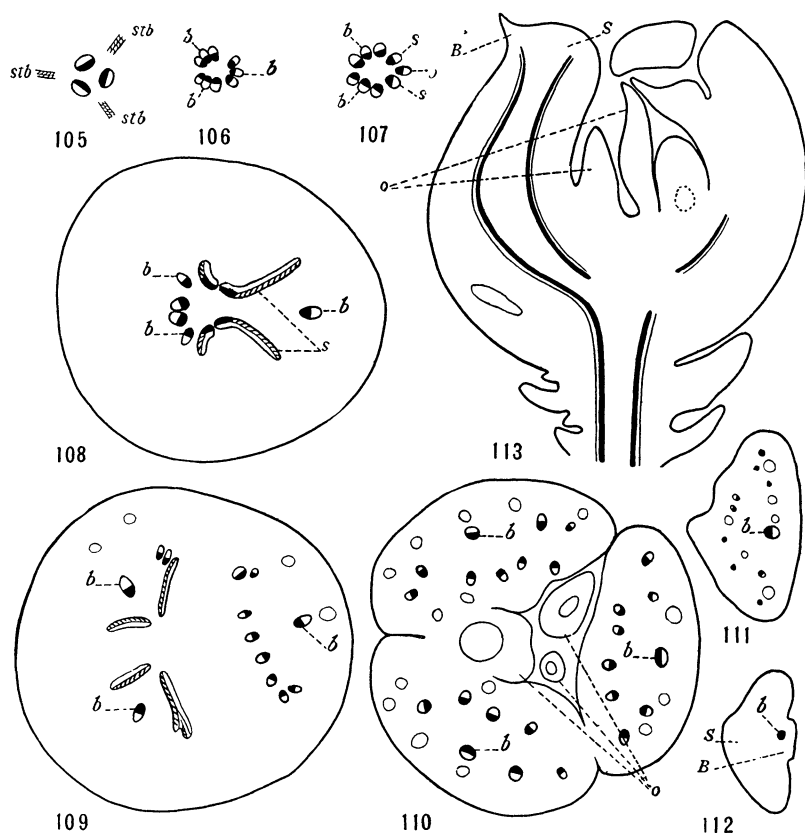


FIGS. 105–113.—*Juniperus communis:* figs. 105–110, course of bundles from base of strobilus to middle of three sporophylls; sporophylls closely coalesced at base; some of scale bundles come to lie in same plane as bract bundle (*b*); figs. 111, 112, transverse sections of tip of sporophyll, bract apparent as small ridge (*B*); fig. 113, longitudinal section of strobilus; *o*, ovule; *stb*, sterile bracts below strobilus; ×16.

pass into the free portion of the bract at each side of the bract bundle and have the same orientation of parts as the bract bundle. The ending of each bundle is accompanied by short irregular tracheids. The scale bundle may arise in closer proximity to the

bract bundle; in the lower sporophylls scale and bract supplies spring from the base of the gap as one large bundle which breaks into three; these latter supply the sporophyll parts as described before.
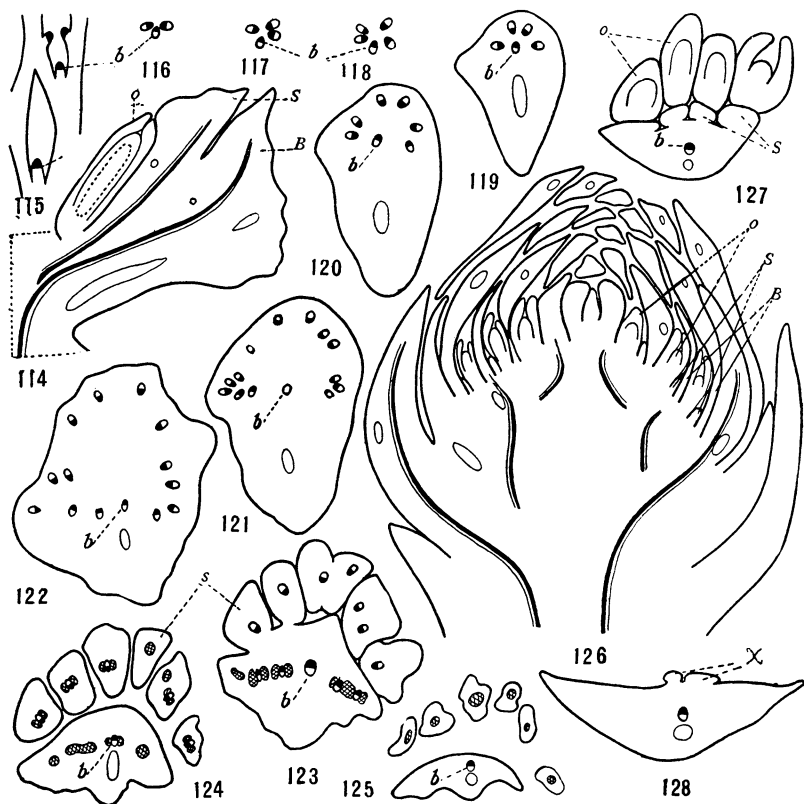


FIGS. 114–128.—*Cryptomeria japonica:* fig. 114, longitudinal section of sporophyll; fig. 115, origin of bract (*b*) and scale bundles in upper part of strobilus distinct, in lower part united (*bs*); figs. 116–125, transverse sections, further course of bundles in sporophyll; bract bundle (*b*) remains undivided, some of scale bundles come to lie in same plane as bract bundle (figs. 121, 122); lobes of scale separate from one another and from bract, each lobe receiving usually one bundle; remaining scale bundles enter free portion of bract (figs. 123, 124); bundles end in large irregular tracheids; ovules not represented; ×7; fig. 126, longitudinal section of young strobilus, scale (*S*) appears as small lobes between bract (*B*) and ovules (*o*), ×16; fig. 127, transverse section of young sporophyll, showing bract (*B*), four lobes of scale (*S*), and ovules (*o*); fig. 128, transverse section of one of uppermost sterile sporophylls, showing outgrowths similar to lobes of scale in fig. 127, ×34.

The strobilus of *Taxodium distichum* possesses the same general characters as described for *Cryptomeria japonica*.

The strobilus of *Cunninghamia Davidiana* (figs. 129–141) is composed of a relatively large number of sporophylls. The scale is united to the bract, with the exception of a small edge distal to the insertion of the three inverted and slightly winged ovules. The vascular supply to the sporophyll departs from the cylinder gap as one large bundle; this bundle soon divides more or less definitely into three; a further division takes place until a row of fifteen or more normally oriented bundles results in the expanded part of the sporophyll. In the earlier course of the branching of the bundles weak strands separate from the lateral bundles and swing around 180° so as to lie on the dorsal side of sporophyll; some of these strands fork, so that an upper row of five or six inverted bundles results; some of these bundles may begin blindly; near the insertion of the ovules one or two strands bend toward the chalaza and end there or a short distance behind the chalaza. Owing to the fact that the bundles in the lower row adhere more or less in the earlier course of division, it is difficult to determine whether the median of the three first bundles passes undivided into the narrow portion of the bract. It is accompanied, however, by branches from the lateral bundles for some distance into the free portion of the bract. At the tip and base of the strobilus are sterile sporophylls. These have a vascular anatomy similar to that of the fertile sporophylls, with the exception of the absence of the upper inverted bundles in the former. Neither scale nor ovules are present, but in place of these appear slight excrescences with different staining reactions.

## ARAUCARINEAE

The ovulate strobilus in the Araucarineae is composed of numerous spirally arranged and closely compacted sporophylls. Each sporophyll bears one inverted ovule, which is imbedded in the sporophyll tissues in *Araucaria*, and naked and winged on one side in *Agathis*. Another feature of the Araucarineae of significance in this connection is the branching of the sporophyll bundle in the
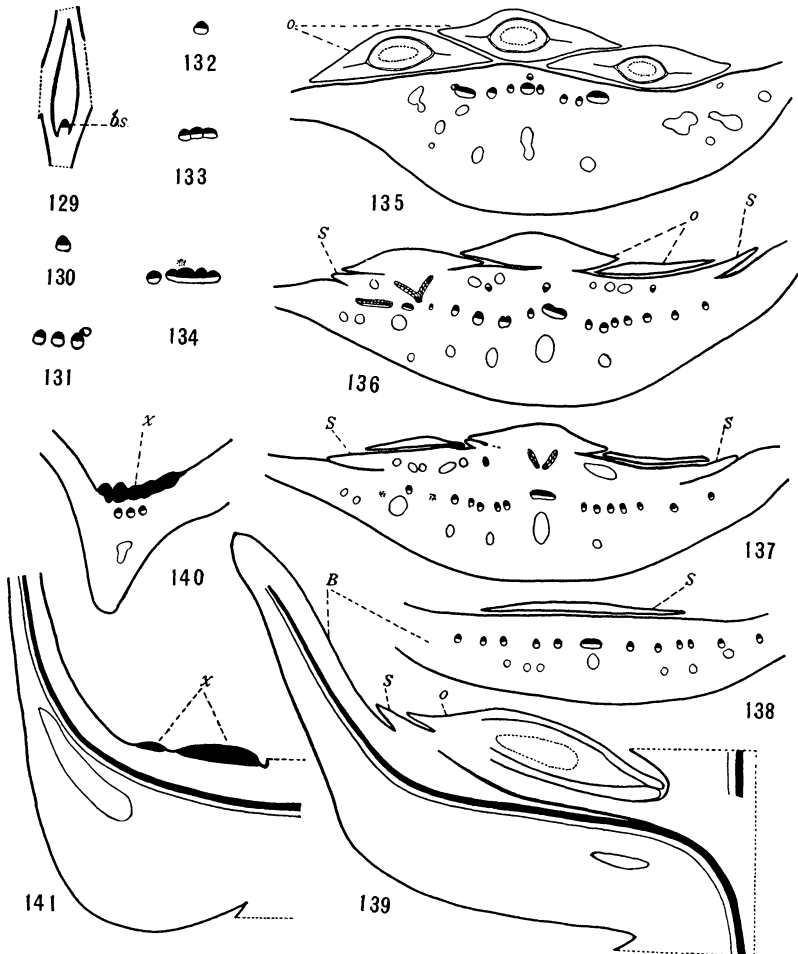
FIGS. 129–141.—*Cunninghamia Davidiana:* fig. 129, vascular supplies to bract and scale leave cylinder gap as one bundle (*bs*); figs. 130, 131, and 132–134, splitting up of single bundle; figs. 135–138, transverse sections of sporophyll small strands split off from lower series or begin blindly (fig. 134, dots) and come to lie on dorsal side of sporophyll; the majority of these small bundles finally bend toward chalaza of ovules and end there; the majority of lower bundles enter free portion of bract (fig. 138, *B*) beyond insertion of scale (*S*); fig. 139, longitudinal section of sporophyll, scale (*S*) appears as flap beyond insertion of ovules (*o*); fig. 140, transverse section of sterile sporophyll near tip of strobilus, dark stained elevations (*x*) taking place of scale and ovules; fig. 141, longitudinal section of sterile sporophyll at base of cone, similar outgrowths (*x*) as in fig. 140;  ×7.

vegetative leaf. This is a characteristic which so far as investigated occurs outside the Araucarineae only in *Podocarpus Nageia*.

The sporophyll of *Araucaria* is characterized by the so-called ligule, which there is good reason to believe is homologous with the scale described in the foregoing groups. In the young strobilus of *Araucaria Rulei* and *Araucaria Balansi* the comparatively small ligule is attached to the bract at its base only, the greater portion being free. In the older strobilus it is free only at the tip. Distal to the line of coalescence of bract and scale the bract remains thick and wide, then becomes narrow and stiff, resembling the bracts at the base of the strobilus.

The vascular supply to the sporophyll of *A. Balansi* (figs. 142–154) arises as a single bundle near the base of the gap in the strobilus cylinder. In the middle of the cortex the single bundle divides into two unequal parts, the smaller of which twists through an angle of 180° so as to lie above the parent bundle with its xylem facing the xylem of the latter. The upper bundle may or may not divide at this stage; the lower bundle divides into two or three; in case of two, one bundle soon divides and a median lower bundle is formed. The lateral bundles divide actively; some of the resulting bundles become inverted and lie on a level with the upper bundle, others normally oriented come to lie on a level with the lower median bundle. Where the sporophyll broadens, branches with normal orientation enter the wings. Behind the ovules the bundles of the upper series begin to converge in groups, and finally end in masses of irregular tracheids. A bundle is sometimes found to continue almost to the free portion of the ligule. Where the bract becomes narrow, the lower bundles also end, with the exception of about three median ones which extend into the slender portion. In the lowest sporophylls, where the ovule and scale are poorly developed or absent, the upper bundles are weak and few in number, or wanting.

In the other forms investigated, *A. Rulei* (figs. 155–161) and *A. excelsa*, the general features are as in the above-described species.

The strobilus of *Agathis australis* (figs. 162–170) is composed of numerous sporophylls which are very closely packed, probably owing to the shortening of the strobilus axis. A ligule, as found in
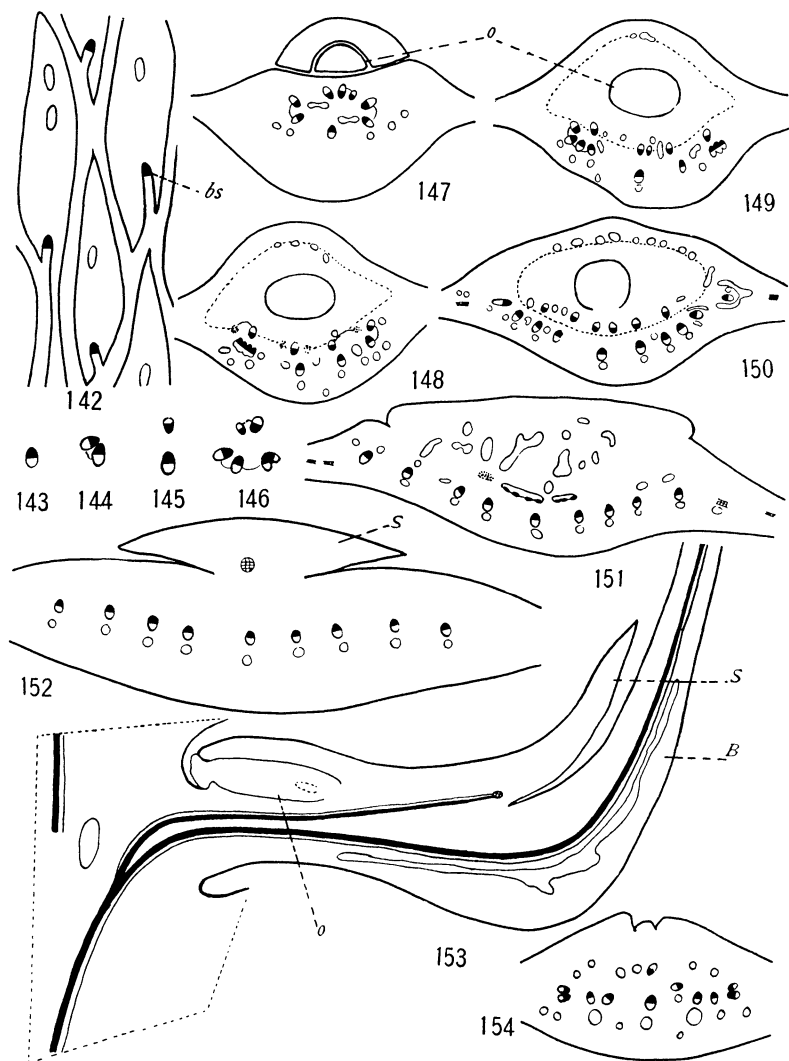
FIGS. 142–154.—*Araucaria Balansi:* fig. 142, vascular supply to sporophyll springs from single strand near base of cylinder gap; figs. 143–146, course of bundles in cortex; figs. 147–152, transverse sections of sporophyll, lines drawn between bundles indicate last division; upper bundles run together in groups and end in large irregular tracheids (fig. 151); one persists almost to free portion of scale (fig. 152); fig. 153, longitudinal section of sporophyll (*S*, scale or ligule; *B*, bract, *o*, ovule); fig. 154, transverse section of sterile sporophyll at base of strobilus, upper bundles few; ×8.5.

*Araucaria*, is absent, but the general appearance of a slight eleva-
tion behind the ovule suggests the possibility of a fused body.
The vascular supply begins as a single stout trace a little to one
side at the base of the short wide cylinder gap.    The trace increases
in size, and in the outer one-third of the cortex a branching begins
which in the lamina of the scale results in about thirteen bundles.
About half-way between the insertion of the sporophyll and the
insertion of the ovule a small strand splits off from one of the median
bundles, swings around 180°, and becomes an inverted bundle
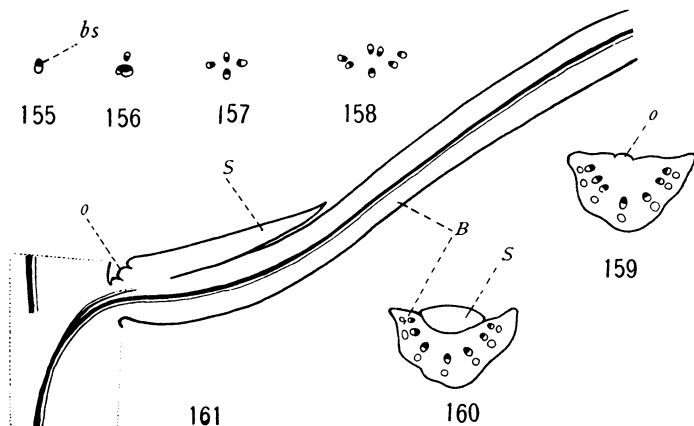


FIGS. 155–161.—*Araucaria Rulei*, young sporophyll: figs. 155–160, course of
bundles from strobilus axis to free portion of bract, upper bundles differentiated in
cortex and base of sporophyll (*B*, bract; *S*, scale; *o*, ovule); fig. 161, longitudinal
section of sporophyll; ×8.5.

opposite its sister bundle.    The inverted strand may fork, and also
inverted strands may spring from several of the median lower bundles
and these strands may divide so that the number of upper bundles
varies from one to several.    In any case, each of the upper
bundles, after giving off a phloem-like strand to each ovule, ends in
large irregular tracheids.

### PODOCARPINEAE

In most of the Podocarpineae a definite strobilus is absent, the
fructification consisting in most cases of one or two fertile sporo-
phylls.    In many forms there is a tendency for some part of the
fructification to mature fleshy.
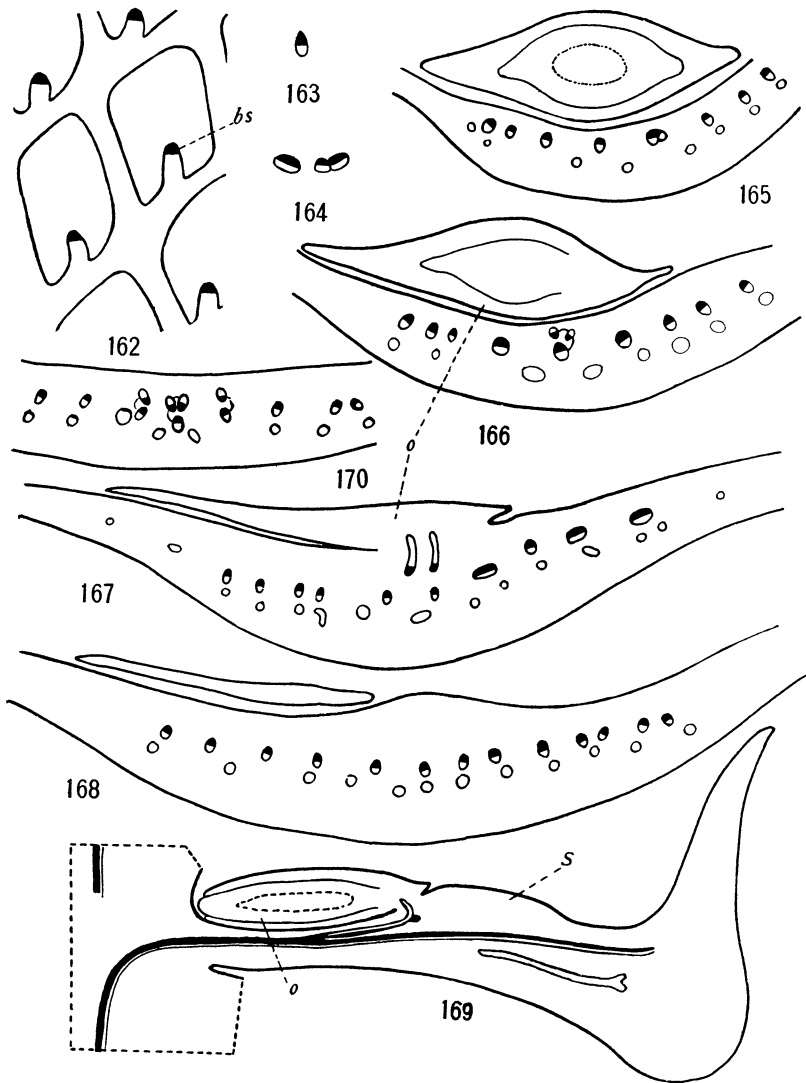
FIGS. 162–170.—*Agathis australis:* fig. 162, vascular supply to sporophyll springs from single strand near base of cylinder gap; figs. 163–168, course of bundles in cortex and sporophyll, a bundle springs from a median bundle, becomes inverted (fig. 166), then breaks into two branches which enter chalaza of ovule (fig. 168), ×8.5; fig. 169, longitudinal section of sporophyll, an elevation appears distal to insertion of ovule; fig. 170, transverse section of sporophyll, inverted bundles have sprung from three of median lower.

In a species of the subgenus *Eupodocarpus* (figs. 171–182) the ovule-bearing branch is a dwarf lateral branch bearing at its tip one and occasionally two fertile sporophylls, and a few small bracts some distance below. The single inverted ovule is imbedded in the tissues of the "epimatium," which there is evidence for believing to be homologous with the ovuliferous scale in other conifers. At maturity the portion of the fruiting branch between the fertile sporophylls and the upper sterile bracts becomes fleshy.
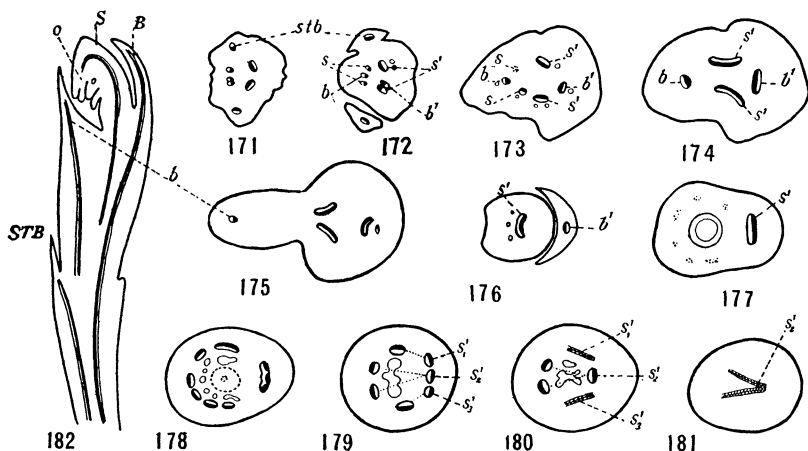


FIGS. 171–182.—*Podocarpus* (sp. of *Eupodocarpus*): figs. 171–181, transverse sections from base of uppermost sterile bracts (fig. 182, *STB*) to tip of strobilus; *stb*, bundles supplying sterile pair of bracts; *b*, bundle supplying sterile bract opposite fertile sporophyll; *s*, bundles inclining toward sterile bract then ending; *b¹*, bundle supplying bract of fertile sporophyll; *s¹*, two bundles uniting into one enter scale of fertile sporophyll where the single bundle breaks into three (fig. 179, $s^1{}_1$, $s^1{}_2$, $s^1{}_3$); distal to chalaza each of three bundles bends to pass down dorsal side of ovule (figs. 180, 181; fig. 179; dotted lines between bundles indicate that one bundle is a continuation of the other); fig. 182, longitudinal section of strobilus; ×7.

The vascular anatomy was investigated only in cases of one fertile sporophyll. The vascular supply of the branch axis, after the traces to the sterile bracts have gone out, consists of three small and three large bundles. The median of the three smaller bundles enters what in the young stages appears like a bract opposite the fertile sporophyll; the two small lateral bundles bend in the same direction as the small median bundle, then end. The

median of the three larger bundles supplies the bract of the fertile sporophyll; each of the lateral bundles twists so as to lie with xylem facing the bract bundle, then the two unite into one bundle which proceeds into the scale. The single bundle increases in size, and on nearing the chalaza of the ovule breaks into three; at the base of the ovule each of the lateral branches curves over and passes downward in the tissues of the scale flanking the ovule. The median bundle proceeds slightly farther, then curves over the base of the ovule, and at the same time breaks into two branches which pass downward in the portion of the scale on the dorsal side of the ovule. The recurved branches of the scale supply fork so that
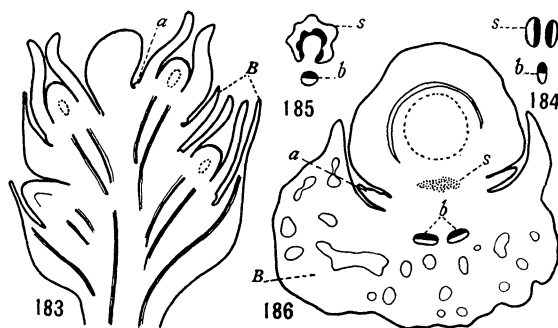


FIGS. 183–186.—*Phyllocladus alpinus:* fig. 183, longitudinal section of young strobilus, aril (*a*) appearing around the base of the ovule; figs. 184, 185, scale (*s*) bundles unite to form a semicircle; fig. 186, transverse section of an older sporophyll, bract bundle (*b*) forks in this instance, scale bundle (*s*) ends at base of ovule; ×61.

in cross-section a ring of bundles with xylem facing outward surrounds the ovule.

In another species of *Podocarpus* investigated the scale bundle divides into two instead of three branches. Each of these two curves at the chalazal end of the ovule and passes downward, one at each side of the ovule. The crests of the two curves are connected by irregular xylem cells, and a strand of similar tissue extends from each crest outward into the protuberance on the scale behind the ovule.

*Phyllocladus alpinus* (figs. 183–186) consists of a globose strobilus of few sporophylls. The ovule is sessile in the axil of the bract. The vascular supply to the bract springs from the base

of the gap.   Two bundles from the sides of the gap unite to form a semicircle which ends at the base of the ovule.

## TAXINEAE

Perhaps the most outstanding features of the Taxineae in this connection are the distinctly terminal ovule in some forms and the development of the aril in the later stages.

In *Taxus baccata* (figs. 187–196) the bud of the primary fertile and dwarf branch develops in the axil of a leaf of a long branch of the first season's growth;  the second season the ovule matures. Near the tip of the primary fertile and dwarf branch is a secondary dwarf branch bearing a few decussate pairs of bracts and terminally an ovule.   Occasionally two secondary dwarf ovule-bearing branches are produced, one at each side of the terminal vegetative bud of the primary branch.   Beneath the ovuliferous branch or branches the primary shoot is covered with scalelike bracts.   The growth of the terminal vegetative bud of the primary shoot is usually arrested by the active development of the secondary ovuliferous branch, so that the latter appears to be terminal.   Ovules are found maturing on the second, third, and fourth seasons' growth, instead of on the second season's only.   This implies that the ovule in some cases fails to mature the second season, or that the vegetative bud of the primary dwarf branch may resume activity and produce other ovuliferous branches;  the latter seems most probable;  also the presence of branch scars on the older and more elongated dwarf shoots suggests that the latter conclusion may be drawn.

After the bundles to the upper sterile bracts have either passed into their respective appendages or have ended before entering the latter, the vascular supply of the axis of the ovule-producing branch consists of four bundles.   These bundles unite in pairs, one bundle from each side of the bract bundle of the next lower pair, and not one from each side of the bract of the last pair as is usually the case where the united bundle is to supply some axillary structure.   The xylem creeps around the phloem in each of the two bundles formed.   Sometimes one of the four bundles in the axis ends, whereupon the odd bundle behaves like the fused bundle
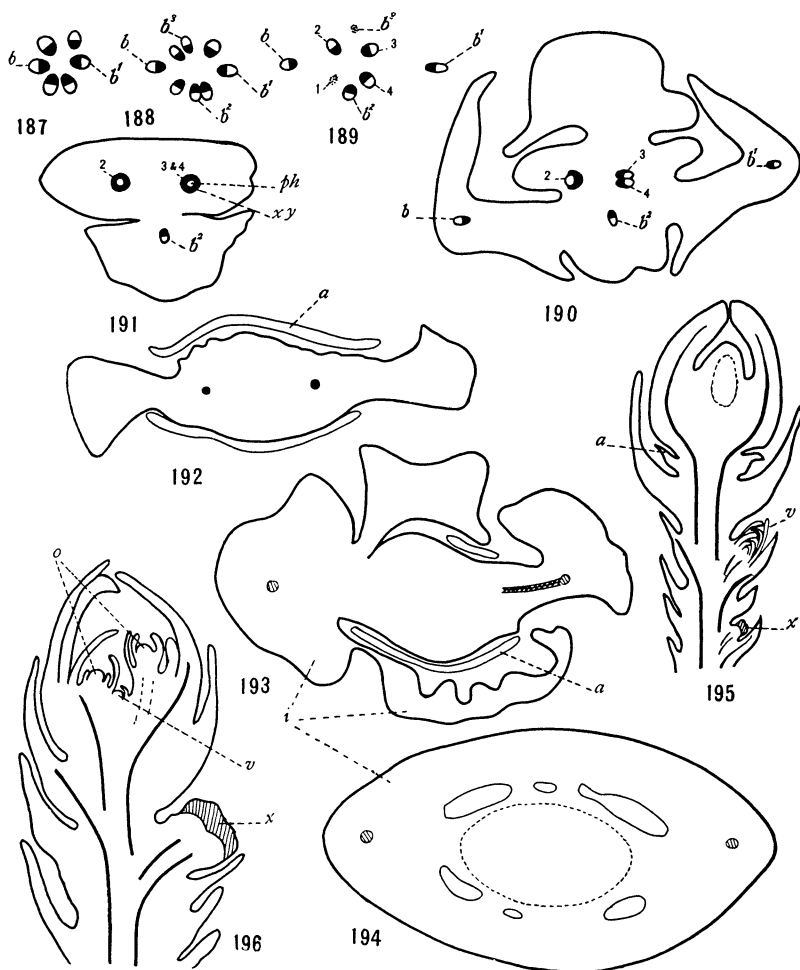
FIGS. 187–196.—*Taxus baccata:* figs. 187–194, transverse sections upper part of fertile branch to middle or ovule; $b$, $b^1$, bundles to supply pair of bracts; $b^2$, $b^3$, bundles to supply uppermost pair of bracts; $b^3$ ends before entering bract; 1, ends in axis; 2, xylem surrounds phloem; 3, 4, unite into one bundle, xylem surrounds phloem (fig. 191), the two bundles continue as weak strands of xylem cells in base of each wing of ovule, xylem cells are soon replaced by elongated slightly thickened cells without true xylem markings, ×16; fig. 195, longitudinal section of fertile branch, terminal vegetative bud ($v$) is turned aside by rapidly growing ovule bearing branch; $x$, scar left by vegetative or fertile bud or branch, ×7; fig. 196, young fertile branch showing two lateral ovule-bearing branches and a terminal vegetative bud ($v$); $x$, scar as in fig. 195, ×16.

(figs. 183, 186).   At the base of the ovule each bundle passes into a mass of short irregular tracheids of large caliber.   From each mass arises a small strand consisting of poorly developed xylem soon replaced by elongated thickened cells without xylem markings. Each strand passes upward in the thickened ridge of the ovule.

## Discussion

Assuming that the megasporophyll in all the forms is a composite organ, consisting of bract and axillary scale, the investigated forms may be divided into four general groups based on the relation of bract and scale to one another.

In the first group the bract and scale are separate almost to the base of the appendage and both are about equally prominent. Here belong *Keteleeria* (fig. 36), *Pseudotsuga*, species of *Abies*, and species of *Larix*.

In the second group the bract and scale are separate as in the first group, but the bract, at least in the later stages, is much less prominent than the scale, and in certain instances appears distinctly to be on its way to obliteration.   In this group belong species of *Abies* (2), species of *Larix*, *Tsuga*, *Picea*, *Pinus* (figs. 1, 2), and species of *Podocarpus* and *Dacrydium* (4); *Cedrus Libani* (2) and the lower sporophylls of *Pinus Banksiana* (fig. 2) show the bract in process of extinction.   In species of *Podocarpus* the scale has folded toward its dorsal side, thus forming the second integument or epimatium of the inverted ovule (fig. 182).

In the third group the bract and scale are considerably to completely welded, but the fused structure shows some evidence of its double nature.   Within this group are *Sciadopitys* (2), *Sequoia* (2), *Cunninghamia* (fig. 139), species of *Arthrotaxis* (1), *Cryptomeria* (fig. 114), *Taxodium*, *Thuja* (fig. 85), *Cupressus* (fig. 59), *Chamaecyparis* (fig. 102), *Juniperus* (fig. 113), *Araucaria* (fig. 153), and *Podocarpus dacrydioides* (4).   In young strobili of *Araucaria Rulei* (fig. 161) and *Cryptomeria japonica* (fig. 126) the bract and scale are distinct almost to the base, and the fused portion becomes comparatively large in the subsequent development of the organ. In *Cupressus Benthamii* (fig. 58), *Thuja occidentalis*, *Chamaecyparis Lawsoniana* (fig. 103), and *Juniperus communis* the scale in the

young strobilus is one with the bract and becomes evident in the later stages by the comparatively rapid growth of the tissues on the dorsal side of the composite organ.

In the fourth group there is no external evidence of more than one organ. Into this group fall *Arthrotaxis selaginoides* (**1**), *Agathis* (fig. 169), *Saxegothaea* (**5, 8**), *Phyllocladus* (fig. 183), *Taxus* (fig. 191), *Torreya* (**6, 7**), and *Cephalotaxus* (**6, 7**). It should not be surprising to find forms in which the welding has taken place beyond the recognition of more than a single structure when one considers to what extent this process has taken place in *Chamaecyparis*, *Juniperus*, *Thuja*, *Cunninghamia*, and *Podocarpus dacrydioides* (**4**). The low cushion behind the ovule in *Agathis australis* suggests the complete fusion of a scale to a large bract; a similar fusion is nearing its completion in *Cunninghamia Davidiana*.

On the basis of vascular anatomy the investigated sporophylls fall into two general groups.

In the first group the bract and scale supply arises as separate bundles in the cylinder gap. In this group belong in general those forms in which the two sporophyll parts are separate and fairly well developed, as the seed-producing sporophylls of *Pinus Keteleeria*, *Picea*, *Larix*, *Tsuga*, *Pseudotsuga*, and *Abies* (**2**). To this group belong also many in which the two sporophyll members present considerable to complete fusion, as *Araucaria Bidwilli* (**1, 3, 10**), *Chamaecyparis Lawsoniana*, *Juniperus communis*, and the upper sporophylls of *Thuja occidentalis*, *Cupressus Benthamii*, and *Cryptomeria japonica*. This group includes also some in which the sporophyll is evident only as a single organ, namely *Phyllocladus* and *Cephalotaxus* (**6, 7**).

In *Podocarpus* and *Dacrydium*, where the strobilus consists of one or two sporophylls, and in *Juniperus communis*, the sporophylls receive the final bundles of the axis. There is in these instances no cylinder gap, and the bract and scale supplies, at least in the forms investigated by the writer, result from the division of one of the final bundles in the axis. The early division of the bundle in the tip of the axis perhaps justifies the placing of these forms in this group.

In the second group based on vascular anatomy the bract and scale vascular supplies are more or less intimately united into one bundle which springs from the base of the cylinder gap.

Of sporophylls with parts separate there belong here the lower sporophylls of *Pinus Banksiana, P. maritima,* and *Keteleeria Fortunei* (the ovules in these sporophylls are to greater or less extent abortive), and *Cedrus Libani* (2). Of the sporophylls with parts considerably united there fall into this group those of *Cunninghamia, Arthrotaxis laxifolia* (1), most species of *Araucaria* (1, 3, 6, 7, 9, 10), and the lower sporophylls of *Cryptomeria japonica, Cupressus Benthamii,* and *Thuja occidentalis.* Most of the apparently simple sporophylls are included in this group, as those of *Agathis, Saxegothaea* (5, 8), and *Arthrotaxis selaginoides* (1).

The degree of welding of the bract and scale vascular supplies varies considerably. In *Arthrotaxis selaginoides, Agathis, Araucaria,* and *Saxegothaea* the two remain united into one bundle for greater or less distance in the cortex; in most of the others the single bundle divides early; but in many cases, where the two sporophyll parts have fused extensively, branches of the scale supply swing about to lie on the ventral side of the appendage at each side of the bract bundle. This fact is well illustrated in *Thuja occidentalis, Juniperus communis, Cupressus Benthamii,* and *Cryptomeria japonica.* In *Cupressus Benthamii* and *Cryptomeria japonica* the scale bundles at either side of the bract bundle even accompany the bract bundle into the free portion of the bract.

Bundle distribution is generally directly related to the size of the organ supplied, hence the bundles extend into the most expanded region of the sporophyll, whether that particular region represents bract or scale.

In *Cunninghamia, Araucaria,* and *Agathis,* in which absence of sporophylls with separate bract and scale supplies makes comparison impossible, it is difficult to determine with certainty what is bract and what is scale supply. The matter is further complicated by the presence in the last two genera of a branching bundle in the vegetative leaf, a condition which probably implies a branching bract bundle in the bract of the sporophyll as well. And, further, *Cupressus Benthamii* and *Cryptomeria* have clearly shown

that the final destination of a bundle does not always determine to which sporophyll part it belongs. It is to be suspected that the bundle system of *Agathis* and *Araucaria* represents a complex of bract and scale bundles. Judging by the course of events in other conifers with single-veined vegetative leaves, it may be suggested that the large median lower bundle in *Cunninghamia Davidiana* is the bract bundle proper, which is accompanied for some distance into the free portion of the bract by a few scale bundles.

*Taxus* presents some features which perhaps ought to be mentioned. The single ovule is produced terminally on a secondary dwarf branch clothed with a few pairs of decussate bracts. The primary dwarf branch may occasionally become a long branch by the resumption of growth by its terminal bud. In all of the many ovules examined the ovule is flattened transversely to the uppermost pair of bracts. The four final bundles of the branch of the axis which fuse in pairs before entering the two wings of the ovule fuse in pairs across the next lower pair of bracts, and not across the uppermost pair of bracts, a behavior which is contrary to what should be expected if the fused bundle were destined to supply an axillary structure. The dying out of bundles near the tip of the axis and the consequent failure to supply the uppermost bracts or enter into the formation of the ovuliferous supplies, as the case may be, suggest that a general reduction and loss of parts is taking place. The terminal position of the ovule, the flattening of the ovule transversely to the uppermost bracts, and the fusion in pairs of the final bundles of the axis in the definite way to form the two bundles of the wings of the ovule suggest a structure which might result from a process well under way in *Juniperus communis*, namely the fusion of sporophylls to form a single structure. This in *Taxus* would imply the reduction of the ovules to one, the complete fusion of two sporophylls to the integument of the ovule, and finally the reduction of the vascular supply of each sporophyll to the single weak bundle present in the wing of the ovule. In view of the modifications that are apparently taking place in other conifers such a course of events may be possible, but further investigation is necessary.

The ovule of *Phyllocladus glauca* presents a slightly simpler situation than that of *Taxus*. The two bundles beginning from the sides of the gap and ending at the base of the ovule are probably the only vestige of the scale. The aril may be no more than an outgrowth such as appears in connection with the ripening of ovules in the podocarps. The outer integument of *Torreya* may be a more complex organ.

If any probable conclusions can be made concerning the ovulate structure of the Taxineae, they must in any event be preceded by a more thorough investigation of the different forms.

In spite of striking modifications, the origin of the megasporophyll is homologous throughout the conifers. As to the identity of the organ in question there seems nothing new to be added. The gradation from foliage leaves to bracts of sporophylls is so definite in many forms, as in *Larix* and *Pseudotsuga*, that the homology of one with the other need not be questioned. The scale is the organ in doubt. Its axillary position and the origin of the vascular supply when separate from that of the bract justifies the theory that it is some modification of a fertile branch. Through shortening of the axis and rather delayed development of the shoot in general, together with a relatively earlier development of the ovules, the semicircle of bundles at the base of an ordinary shoot failed to form the cylinder, but instead flattened out into an arc and in some cases even into a straight line.

## Summary

1. In the evolution of the ovulate strobilus in members of the Coniferales, two general tendencies are apparent: (1) the reduction in number of sporophylls in the strobilus; (2) the modification of a compound sporophyll into an apparently simple sporophyll; the latter appears in diverse disguises, but in general implies loss of one of the sporophyll members or welding of the two.

2. Strobilus reduction has reached its highest expression in members of the Cupressineae, Taxineae, and Podocarpineae; one type of strobilus reduction is represented by the general sterilization and reduction of parts in the lower sporophylls of *Pinus*.

3. Simplification of a compound sporophyll has been attained to fullest extent in *Arthrotaxis selaginoides, Agathis,* and *Saxegothaea,* and possibly others; an extensive reduction of bract occurs in *Cedrus Libani* and the lower sporophylls of *Pinus maritima;* the scale in *Phyllocladus* is probably reduced so as to be represented only by a distinct ovular supply; the welding of the two organs is complete in *Juniperus communis* and *Chamaecyparis Lawsoniana.*

4. Fusion of bract and scale vascular supplies does not directly parallel fusion of bract and scale.

5. Separate origin of bract and scale vascular supplies occurs most generally in the Podocarpineae and Abietineae; fusion of bract and scale supplies has reached its highest expression in the Araucarineae; both types of bundle origin are represented in the same strobilus in *Cryptomeria japonica, Cupressus Benthamii,* and the lower sporophylls of *Pinus.*

6. The bract bundle in plants with uninerved vegetative leaves divides only slightly if at all; the extent of the scale bundle system is directly related to the size of the organ supplied.

7. The scale bundles in the Abietineae and *Chamaecyparis Lawsoniana* form in the expanded portion of the organ a straight row or arc; in members of the Taxodineae and Cupressineae scale bundles swing around so as to lie at each side of the bract bundle.

8. In *Cryptomeria japonica* and *Cupressus Benthamii* and perhaps *Cunninghamia Davidiana* scale bundles accompany the bract bundle into the free portion of the bract.

9. A branching bundle in the vegetative leaf in *Araucaria* and *Agathis* probably implies a branching bundle in the bract of the sporophyll; the vascular system in the megasporophyll is probably a complex of bract and scale bundles.

10. In species of *Podocarpus* the scale bundles continue in the portion of the scale folded toward the dorsal side, forming the epimatium of the ovule.

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